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## Synopsis of *Zodesmus*, a genus of Papuan millipeds (Polydesmida: Platyrrhacidae: Psaphodesmini)

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### ABSTRACT

*Zodesmus* is redefined on the basis of several gonopod characters, and eight species listed from the generic range in the Papuan region. The synonymy of this name and *Eutrachyrhachis* is discussed; several species are illustrated, and the new species *Z. astromontis* is described from the Finim tel region of Papua New Guinea.

The present part of an ongoing treatment of the platyrrhacid tribe Psaphodesmini is devoted to a brief overview of the genus *Zodesmus*, set up by Cook in 1896 and thus one of the oldest named groups within the tribe. The original generic concept was based on the single species *Stenonia tuberosa* Pocock (1893), and justified by a succinct verbal diagnosis, one half of a key couplet:

“Copulatory legs with three prongs; sterna not spined, lateral margins of carina with 4-6 rounded tubercles; posterior corner of carinae not produced into a sharp spur; anterior and posterior margins of carinae smooth; Genus *Zodesmus*, type *Z. tuberosus* (Poc.), Ki Islands.”

Without illustrations, any generic name proposed with such a diagnosis was considered to be essentially a *nomen nudum* by Graf Attems, at whose hands the family Platyrrhacidae experienced virtually most of its subsequent development. His definitive monograph in 1938 referred 90% of the known species to a single genus, cleft into five subgenera, and *Zodesmus* remained an obscure synonym until 1962 when, after having studied several relevant species, I proposed to revive it as a valid taxon. My 1980 “Classification” again listed *Zodesmus*, this time with Pocock’s genus *Eutrachyrhachis* entered as a junior synonym but without a word of

explanation. Having the opportunity to renew a long dormant interest in the tribe Psaphodesmini, as expressed in the form of short generic revisions, I belatedly take the opportunity to document my current perception of *Zodesmus* as another increment on the way to an eventual treatment of the entire family Platyrhacidae.

#### ACKNOWLEDGMENTS

For the loan of, or access to, relevant material consulted during the preparation of this review, I am indebted to Keith Hyatt, The Natural History Museum, London (BMNH), Dr. Bernd Hauser, Museum d'Histoire Naturelle, Genève (MHNG) and Dr. Gerhard Pretzmann, Naturhistorisches Museum, Vienna (NMW). Mr. Phillip J. Chapman generously presented me with numerous specimens collected by him during the 1975 British Speleological Expedition to Papua New Guinea.

#### TAXONOMY

### Family Platyrhacidae

#### Tribe Psaphodesmini

This taxon was proposed as a subfamily by Cook (1896) for the reception of the three new genera *Psaphodesmus*, *Zodesmus*, and *Derodesmus*. It was not subsequently recognized until 1980, when I assigned it tribal rank, adding the later-proposed genera *Pleorhacus*, *Parazodesmus*, *Ozorhacus*, and *Erythracus*, and removing *Derodesmus* to the category of "uncertain status". All of these nominal taxa are confined to the Papuan Region, that is, the islands east of Wallace's Line. Many species were added during the period 1899-1945, largely by Attems and Chamberlin, and mostly under the name *Platyrhacus*. In 1938 *Psaphodesmus* resurfaced as a subgenus of that all-embracing name, in a general way corresponding to the content of Psaphodesmini as I now define it.

The platyrhacid fauna of New Guinea is extensive and diverse, and application of a fairly inclusive generic concept based on gonopod characters shows promise in the direction of an adequate synthesis. The inaugural stage of a tribal reclassification appeared in 1997, as a revision of the genus *Parazodesmus*, in which a proposed symbolic nomenclature for the various elements of the gonopod telopodite was outlined. The point was made, that even with a stringent generic concept, species could be distinguished by variations in body form as well as within the context of gonopod form. Extension of the basic premise into related species has permitted recognition of numerous nominal genera, although in many cases restudy of type material has been a prerequisite, and continues to impede a desired rate of progress. Synopses of *Ozorhacus*, *Psaphodesmus*, and several other genera are currently in

preparation, in addition to the genus treated herein. Several additional new genera will also be required to accomodate various extremes of psaphodesmid diversity.

Genus *Zodesmus* Cook

*Zodesmus* Cook, 1896, *Brandtia*, 1: 3. Monobasic. Type species: *Stenonia tuberosa* Pocock, 1893, by monotypy and original designation.

*Zodesmus*: Hoffman, 1962, *Ann. & Mag. Nat. Hist.*: (13) 5: 23; 1980, *Classification of the Diplopoda*, p. 163.

*Eutrachyrhachis* Pocock, 1897, *Ann. & Mag. Nat. Hist.*, (6) 20: 441. Proposed with two new species. Type species: *E. victoriae* Pocock, by original designation. Synonymized by Hoffman, 1980.

DEFINITION: A genus of small to moderate-sized, coarsely tuberculate species in which the gonopod telopodite is not torsate dextrally as in other psaphodesmine taxa, the apical half curved *mesad* and the entire length of the prostatic groove visible in mesal aspect. Gonopod processes **b** and **e** missing, process **c** larger than **a** and

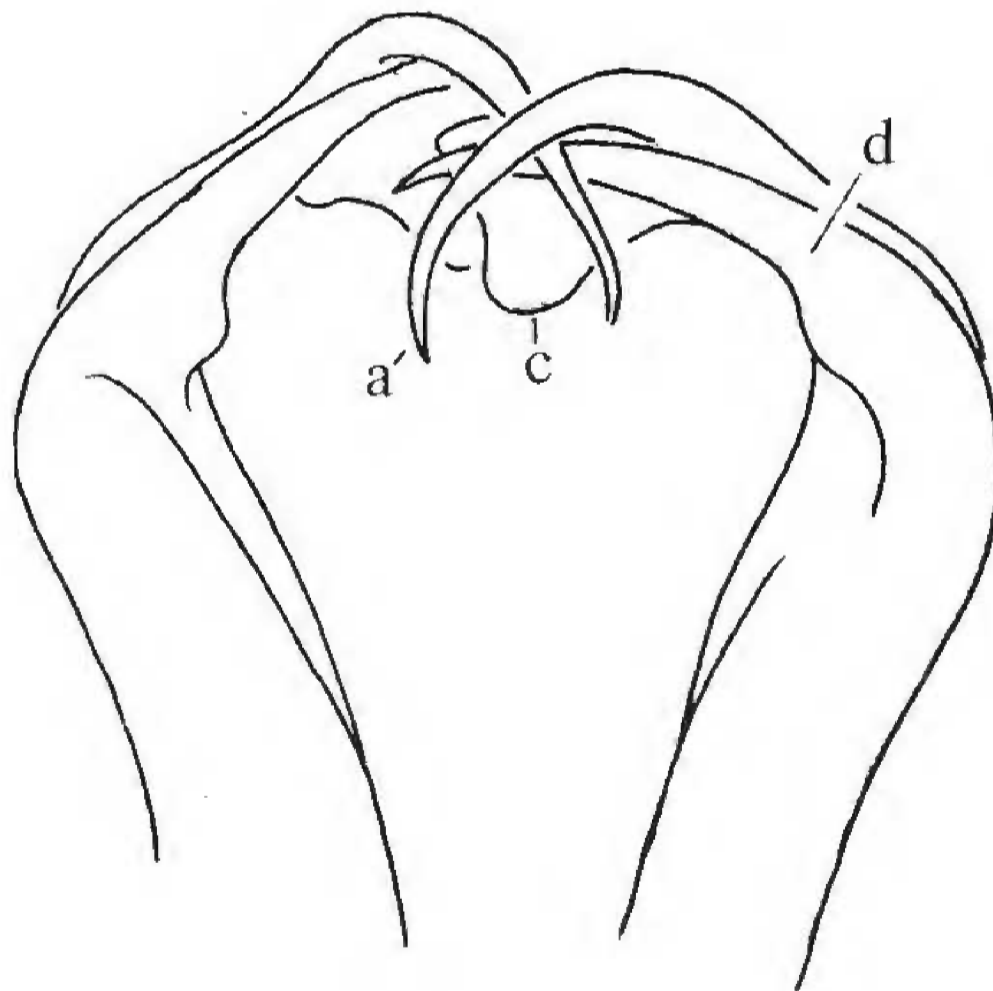


Fig. 1. *Zodesmus astromontis*, new species. Distal half of gonopods in natural resting position, ventral aspect.



broadened distally; process **d** long, slender, and lying parallel to **a** for most of its length. Gonopod formula: (**a**, **C**) **D**. Coxae with several dispersed, simple setae only. Gonopods long, *in situ* extending over sternum of segment 6, the apices overlapping as shown in Figure 1.

DISTRIBUTION: The known members of this genus are restricted to New Guinea, and the Kei and Aru archipelagos.

SYNONYMY: Pocock's taxonomic work was typically so thorough and careful, it is the more remarkable that his 1897 paper on "New Genera and Species of Millipedes of the family Platyrhachidae. . ." was largely faithful to the title and referred to only a few species already known from the Indoaustralian Region. As a result a number of species which might have been placed in some of the new genera were passed by in silence, including many named by Pocock himself. Although five of the genera proposed by Cook in 1896 were admitted, *Zodesmus* was not, nor were the claims of *Z. tuberosus* to be considered taken into account with the proposal of *Eutrachyrhachis*, for what reason I cannot surmise. In any event, I think that the figures given here for *tuberosus* and *margaritatus* support my contention that these species are congeneric. Again, since Pocock departed from his normal procedures by designating *E. victoriae* - known only from a female specimen - as type species of *Eutrachyrhachis*, I am compelled to rely on *margaritatus* as a de facto representative of that generic name although this attaches an element of doubt to its disposal as a junior subjective synonym of *Zodesmus*.

REMARKS: My present concept of *Zodesmus* is somewhat different and more exclusive than proposed in my 1962 paper, emphasizing now the presence of simple coxae seta only, the complete lack of torsion in the telopodite and the distinct enlargement of process **c**.

SPECIES: A considerable number of names have been proposed for species having those three characters, I list them below without prejudice concerning their actual taxonomic status. Some undescribed forms are known, but I introduce here only one, which by its geographic location seems unlikely to become a junior synonym. Clearly a revision of *Zodesmus* is a desideratum for some future investigator, but it is not premature to note that among the nominal species, process **c** takes two forms: one (Fig. 8) in which it is relatively short and broad (*margaritatus*, *lobophorus*), the other (Fig. 3) in which it is long and apically expanded (described by Chamberlin as "malleiform"), which characterizes all of the others.

Material examined by me, and inferences from the literature, suggest that differences between species may be more evidently expressed in peripheral details than in gonopod structure, mandating adequate illustration of paranotal shape and of dorsal ornamentation.



## a. Tuberosus Group

*Zodesmus tuberosus* (Pocock)

Figs. 2-4

*Stenonia tuberosa* Pocock, 1893, Ann. Mag. Nat. Hist., (6) 15: 131, pl. 9, figs. 3-3b.

Male holotype (BMNH) from "Ki-Dulau" [= Kei Dulah, Kei Archipelago, Indonesia].

*Zodesmus tuberosus*: Cook, 1896, Brandtia, 1: 3.

*Cyrtorachis trifidus* Silvestri, 1897, Abh. Ber. Zool. Anthr.-Ethn. Mus. Dresden, 6(9): 13, fig. 17-19. Male holotype (Mus. Dresden, destroyed) from Aru island, Indonesia. Synonymized by Carl, 1912.

*Platyrrhacus tuberosus*: Attems, 1899, Denks. Akad. Wien, 69: 327.

*Platyrrhacus tuberosus*: Carl, 1912, Abh. Senckenberg. Naturf. Ges., 34: 270.

*Platyrrhacus (Pleorhacus) tuberosus*: Attems, 1914, Arch. Naturg., 80 (A4): 270.

*Platyrrhacus (Pleorhacus) tuberosus*: Attems, 1932, Result. sci. Voy. Ind. or. Neerl. 3 (12):

*Platyrrhacus (Psaphodesmus) tuberosus*: Attems, 1938, Das Tierreich, 69: 275, fig. 312.

Dark brown dorsally, antennae, legs, metatergal tubercles, and lateral margin of paranota yellowish. Length to 45 mm, width to 7.5 mm, the females somewhat larger than males. Collum granulate, with a row of enlarged tubercles along anterior and posterior edges; metaterga granular, with three transverse rows of small, equally-sized rounded tubercles, generally 3-3, 5-5, and 6-6. Paranota moderately declivous in males, more so in females, the dorsum thus notably convex. Lateral edges with 4-7 marginal dentations, without incision near midlength (Fig. 4). Sterna glabrous, with small subcoxal knobs.

Gonopods as in Figs. 2 and 3, distal ends of telopodites curved mesad or even slightly ventromesad, the prostatic groove visible for its entire length in mesal aspect. Process c elongated, curved, subapically broadened, with acuminate tip.

My concept of *tuberosus* is derived from topotypic material (MHNG) labeled only "Kei", but presumably that from the Merton Expedition which Carl had compared with, and found "vollkommen identisch" with, the type of *C. trifidus*. In light of better knowledge of specific differences in platyrrhacids, direct comparison of the types of *tuberosus*, *trifidus*, and *principalis* seems necessary to confirm the status of these three nominal species. Although the holotype of *trifidus* is thought to have been destroyed during World War II, the list of Silvestri types at Portici (Viggiani, 1973) lists a syntype specimen, perhaps a male, in that collection.

The species is known to me only from the Kei and Aru archipelagos.

*Zodesmus sternotrichus* (Attems), new combination

Figs. 5, 6

*Platyrhacus (Pleorhacus) sternotrichus* Attems, 1932, Result. sci. Voy. Ind. Or. Neerl., 3 (12): 17, figs. 25-27. Holotype (Naturh. Mus. Wien) from Sakoemi, New Guinea.

*Platyrhacus (Psaphodesmus) sternotrichus*: Attems, 1938, Das Tierreich, 69: 274, fig. 311.

Dark reddish brown, lateral half of paranota yellowish brown. Width 7.5 mm. Lateral ends of collum rounded, directed obliquely ventrad. 2nd segment not wider than 3rd. Paranota set high on sides and almost horizontal, middorsum only slightly convex. Anterior and posterior edges of paranota smooth, lateral edge with 4-7 large tubercular dentations; ozopore peritreme set about its own diameter from the nearest lateral indentation. Metaterga granular, with three transverse rows of tubercles. Epiproct with compound setae. Sterna finely granular and setose, a unique condition in the genus.

Gonopods (Figs. 5, 6) similar to those of *tuberosus*, process c a little longer and more enlarged apically.

This species is known to me only from its type locality.

*Zodesmus principalis* (Attems), new combination

*Platyrhacus (Pleorhacus) principalis* Attems, 1932, Résult. sci. Voy. Ind. or. Neerl., 3 (12): 18, figs. 28-31, . 51. Holotype (Naturh. Mus. Wien) from Manoembai, Aru Islands, Indonesia..

*Platyrhacus (Psaphodesmus) principalis*: Attems, 1938, Das Tierreich, 69: 274, fig. 311.

Piceus, lateral half of the paranota (or only the larger tubercles) yellowish. Length 40-45 mm, width 6.7-9.0 mm. Lateral ends of collum rounded and declivent. 2nd segment notably broader than the 3rd. Paranota set high on sides, subhorizontal, anterior edge smooth, lateral with 6-8 tubercular dentations, no evident indentation near midlength. Metaterga finely granular, tubercles of the first two rows very inconspicuous and notably smaller than those in the 3rd. Sterna finely and densely granulate, without setae.

Gonopod (Attems, 1932, fig. 30) similar to those of *tuberosus*, but process d shown as widely separated from the common stem (a+c) instead of closely parallel to it.

The broad 2nd segment, reduced dorsal tuberculation, and orientation of gonopod process d suggest that *principalis* is specifically distinct from *tuberosus*.



*Zodesmus fratrellus* (Chamberlin), new combination

*Platyrhacus* (*Psaphodesmus*) *fratrellus* Chamberlin, 1945, American Mus. Nov., 1282: 19, figs. 87, 88. Male holotype (AMNH) from "North New Guinea: [now Irian Jaya, Indonesia]: Prauenbivak."

Coloration not documented. Width of male 7 mm. Collum convex, discal surface with four transverse rows of uniform-sized tubercles. Dorsum convex, the paranota declivous, metaterga granular with three rows of widely spaced tubercles, those in 3rd row largest. Anterior and posterior edges of paranota finely crenulate-denticulate, posterior corners becoming acute from 5th segment; lateral edge with shallow indentation at midlength. Sterna without subcoxal spines or knobs.

Gonopod differing from other species in that the telopodite is notably curved mesad at its midlength, and the common stem (a+c) seems substantially longer than usual, with process d much more widely separated from it.

The curved form of the telopodite suggests that this species may warrant placement in a monotypic group, but as process c appears to resemble that occurring in *tuberosus*, provisional location here is justified.

## b. Margaritatus Group

*Zodesmus margaritatus* (Pocock), new combination

Figs. 7-8

*Eutrachyrhachis margaritatus* Pocock, 1897, Ann. & Mag. Nat. Hist., (6) 20: 442, figs. 16-16a. Two male synypes (BMNH 1896.12.20.12-13) from "Victoria Mountain, New Guinea"; no.1896.12.20.12 has been labeled as lectotype.

*Platyrhacus* (*Pleorhacus*) *margaritatus*: Attems, 1914, Arch. Naturg. 80(A4): 268.

*Platyrhacus* (*Pleorhacus*) *margaritatus*: Attems, 1932, Result. sci. Voy. Ind. or. Neerl., 3 (12): 4.

*Platyrhacus* (*Psaphodesmus*) *margaritatus*: Attems, 1938, Das Tierreich, 69: 276.

Color black, the lateral paranotal dentations and metatergal tubercles clear and shiny. Length 43 mm, width of 5th segment 7 mm. Collum convex, disc medially concave, tumid on each side, granulose, with four transverse rows of tubercles. Paranota of anterior segments declivous, others less so, all coarsely granulate dorsally with intermixed larger tubercles, anterior and posterior edges serrate or denticulate, lateral edges with 2 to 4 large blunt dentations between those on the corners. Metaterga with three rows of tubercles, those of the 3rd row largest. Sterna granulate, without setae.



Gonopods (Figs. 7, 8) with telopodite relatively stout, its distal third less turned ventrad than in *tuberosus*, process c short, broad, not extended beyond curvature of a in dorsal aspect (Fig. 8).

If the type locality is taken to be the well-known Mount Victoria in the Owen Stanley range of eastern Papua New Guinea, a generic distribution throughout the length of the island is defined by known localities.

*Zodesmus lobophorus* (Attems), new combination

Figs. 9-10

*Platyrhacus* (*Pleorhacus*) *lobophorus* Attems, 1914, Arch. Naturg., 80 (A4): 270, figs. 53-55. Male syntype (NMW), female syntype (ZMB) from "Berg am Sepikstrom, 1570 m, Deutsch Neu Guinea."

*Platyrhacus* (*Psaphodesmus*) *lobophorus*: Attems, 1938, Das Tierreich, 69: 272, figs. 307-308.

Uniformly yellowish- to chestnut-brown, paranota somewhat lighter in males, in females only the marginal dentations and tubercles lighter. Length not recorded, width of males 7 mm, of females, 9 mm.

Antennae long and slender, extending back to posterior edge of 3rd segment. Collum narrow, lateral ends acute, surface granulate with scattered tubercles, a row of close-set tubercles along anterior margin. Dorsum only slightly convex, paranota of males large and nearly horizontal, slightly more declivous in females. Metaterga granulate, with three transverse rows of tubercles, increasing in size from 1st to 3rd, those of 1st row indistinct. Paranota posterior to 4th divided into two acute lateral lobes by deep midlength incision, at the base of which the ozopores are located; anterior and posterior edges prominently crenulated. Sterna granulate, without setae or subcoxal spines. Gonopods (Figs. 9, 10) characterized by the large, in dorsal aspect nearly square, distally truncate shape of process c.

The exact location of the type locality is uncertain. The Sepik River achieves an elevation of 1570 m fairly near its headwaters in the region between the Thurnwald and Star ranges, in extreme southwestern West Sepik Province.. I have material from the same general area (vicinity of Telefomin) that appears to be closely related to, if not conspecific with *lobophorus*, although the paranota do not agree in detail with Attems' description.

*Zodesmus atopogon* (Chamberlin), new combination

*Platyrhacus atopogon* Chamberlin, 1920, Bull. Mus. Comp. Zool., 54: 139.

Male holotype (MCZ) from Manokwari, Irian Jaya, Indonesia.

*Platyrhacus atopogon*: Attems, 1938, Das Tierreich, 69: 286 (as "Unsicher Art").

Metaterga uniform light brown, dorsum of prozona deeper blackish brown. Legs and antennae paler, testaceous proximally. Length 37 mm, width 6.5 mm.

Collum convex, granulate, with four transverse rows of tubercles, those of the anterior series closely spaced, the others widely separated. Metazona and paranota densely granulate, with three transverse rows of prominent and widely separated, those of 3rd row largest and projecting beyond caudal edge of segment.

Chamberlin's verbal account of the gonopods clearly depicts the structure typical of this genus: "At the beginning of the distal curve [of the telopodite] a flat, slender acute blade [d] arises which runs mesad and curves but little beyond its base. Dorsad of this the principal strongly curving branch divides near the middle of its length, sending caudad a branch [c] which abruptly expands beyond its base into a plate malleiform in outline, the plate giving rise from its ectocaudal corner to a slender acute style; the process beyond this branch [a] continues as a slenderly pointed style the tip of which curves back ectad. . ."

The occurrence of this species at Manokwari suggests that it is probably not a synonym of the several names proposed by Pocock, Attems, and Chamberlin himself, from more distant localities in New Guinea..

*Zodesmus astromontis*, new species

Figs. 11-16

MATERIAL: Male holotype, male and female paratype (VMNH) from Kumsop tem cave at Finim tel, Western Province, Papua New Guinea; 16 August 1975, P. J. Chapman (British Speleological Expedition), leg..

NAME: For the Star Mountain range, immediately southward of the Finim tel valley.

DIAGNOSIS: The smallest known member of the genus. Collum with four transverse series of low, flat areas of irregular size and shape; tubercles of 3rd row of metaterga much larger than those of the rows 1 and 2, hemispherical in shape. Sterna with distinct subcoxal spines. Process c of gonopods a large rounded lobe, constricted at base.

HOLOTYPE: Adult male, length ca. 28 mm (broken), maximum width 5.3 mm at midbody. Color of preserved specimen dorsally light testaceous brown, probably reddish-brown in life, the paranota and epiproct lighter, a pale pinkish-gray; dorsal tubercles testaceous yellow; legs and antennae clear yellow, becoming darker distally.

Labrum and clypeus nearly smooth, genal convexities and epicranial surfaces indistinctly granular; antennae moderately stout, reaching back to rear of 2nd paranota. Collum (Fig. 11) strongly convex, laterad to tubercles the surface vertical with small declivous lateral lobes; disk with a row of contiguous flattened areas along anterior margin and 4+4 large, elevated subovoid tubercles along posterior; the



surface between with two irregular series of low tubercles of variable shape; all dorsal ornamentation closely spaced, virtually contiguous. Metazona of subsequent segments with paranota initially declivous, b midbody becoming nearly horizontal but set low on sides so dorsum is strongly convex, the surface granular with three rows of large tubercles, those of the first two rows usually 4+4 and subequal in size, those in 3rd row much larger and very high and prominent, typically 3+3, not projecting beyond edge of segment, the latter with a single row of small rounded tubercles. Paranota moderate in size, anterior and posterior edges notably crenulate and ciliate (Fig. 13), lateral edge with large incision at midlength, the ozopore at base of the sinus and facing laterad. Dorsal tubercles of posteriormost metaterga smaller, more irregular, and all about subequal in size. Epiproct of the shape illustrated (Fig. 14), dorsal surface nearly flat and smooth. Setae all simple. Hypoproct trapezoidal, paramedian tubercles conical, the edge between them slightly concave. Sterna granular, narrow, about equal to a coxal length, and produced upward toward coxal bases, produced into a small but distinct projection at each coxal condyle. Sides of metazona and underside of paranota with small acute tubercles, a single row of slightly larger rounded tubercles along the posterior margin. Stigmata unusually large, auriculate, the surface very finely granular, nearly as large as the coxal socket, the edges standing free of metazonal surface, both stigmata subequal in size and shape. Legs long, most of femora visible from above when extended, virtually glabrous except for 10-12 scattered setae dorsally on tarsi. Coxae somewhat incrassate ventrally and extended distad a little beyond prefemoral articulation.

Gonopods (Figs. 15, 16) similar to those of *margaritatus* and *lobophorus*, but outline of process c and arched curvature of a appear to be characteristic.

PARATYPE: Adult female, length ca 41 mm (broken), width 7.5 mm. Color much more defined than in male, dorsally a rich maroon, antennae and legs light brown, labrum yellow. Generally similar to male in structure but paranota smaller and more declivous, resulting in a more convex body form, dorsal tubercles similar to those of male but not so high. Sterna broader, nearly equal to femoral length and almost flat, without median impression and subcoxal spines smaller. Stigmata smaller than in male, and coxae not modified.

REMARKS: The sexual dimorphism in size seems noteworthy. Future work with platyrhacids should devote attention to the structure of the stigmata. Although their increased size appears to be a feature for the entire family, it is possible that diagnostic correlations can be identified at lower levels.

#### c. Group position unknown

##### *Zodesmus victoriae* (Pocock), new combination

*Eutrachyrhachis victoriae* Pocock, 1897, Ann. & Mag. Nat. Hist., 6 (20): 442.

Female holotype (BMNH) from Victoria Mountain, New Guinea.



*Platyrhacus (Psaphodesmus) victoriae*: Attems, Das Tierreich, 69: 281 (as "unsicher Art").

"♀. – Colour black, apices of keels yellowish red; the tubercles clearer yellowish. Dorsal tubercles clearer than in *margaritatus*; margins of keels strongly bidentate, with usually one or more small tubercles between them; the anterior tooth much the largest on the second, third, and fourth segments, the posterior much the largest on the sixteenth, seventeenth, eighteenth, and nineteenth. Caudal process more ovate than in *margaritatus*, the posterior border produced some distance behind the posterior lateral tubercles.

"Measurements in millimetres. – Total length 55; width of second segment 7.5, of fifth 9."

Placement of this species in *Zodesmus* is contingent upon the correctness of Pocock's belief that it is congeneric with *margaritatus*. If not, *Eutrachyrhachis* may need to be revived for at least this one species.

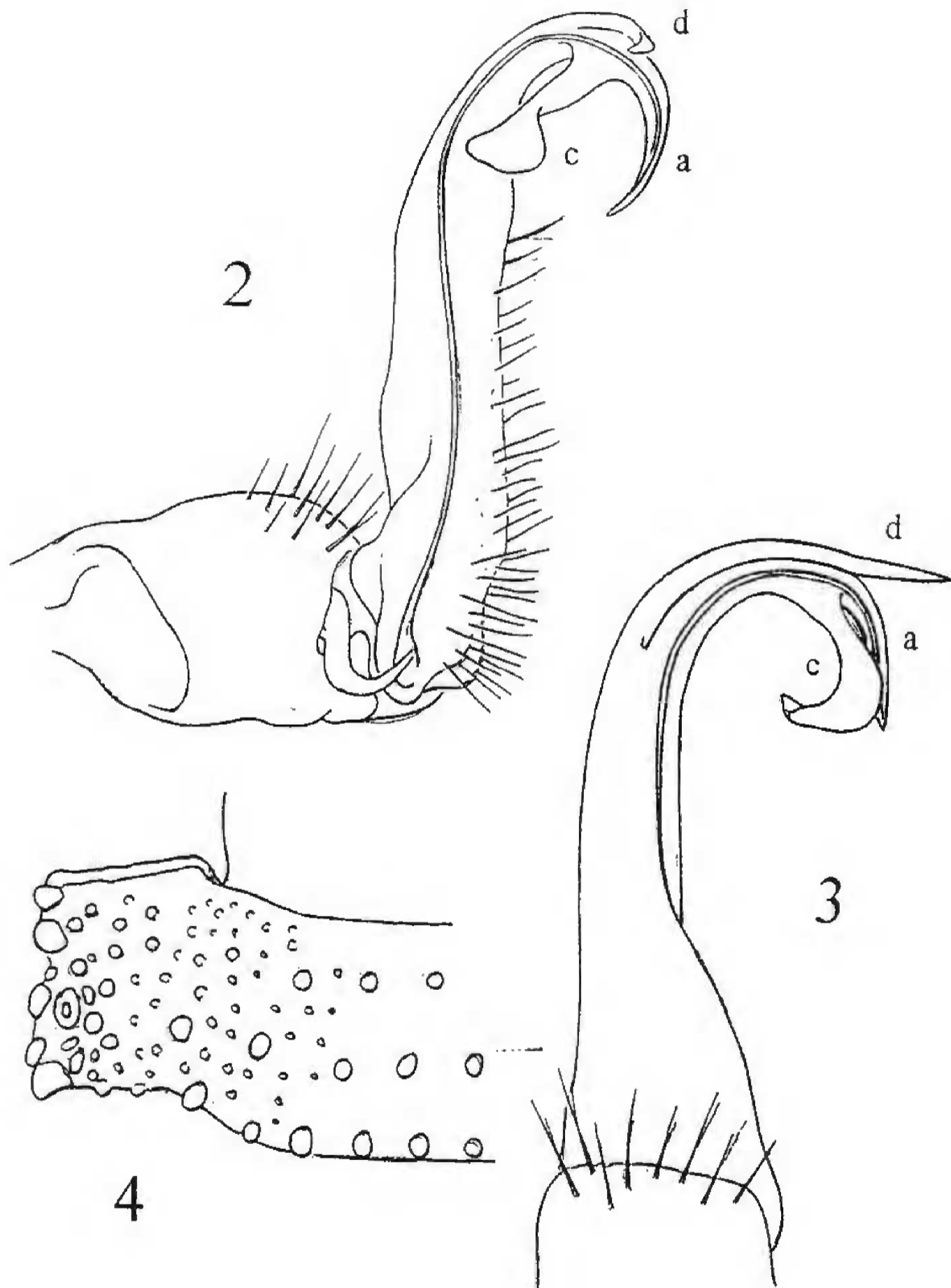
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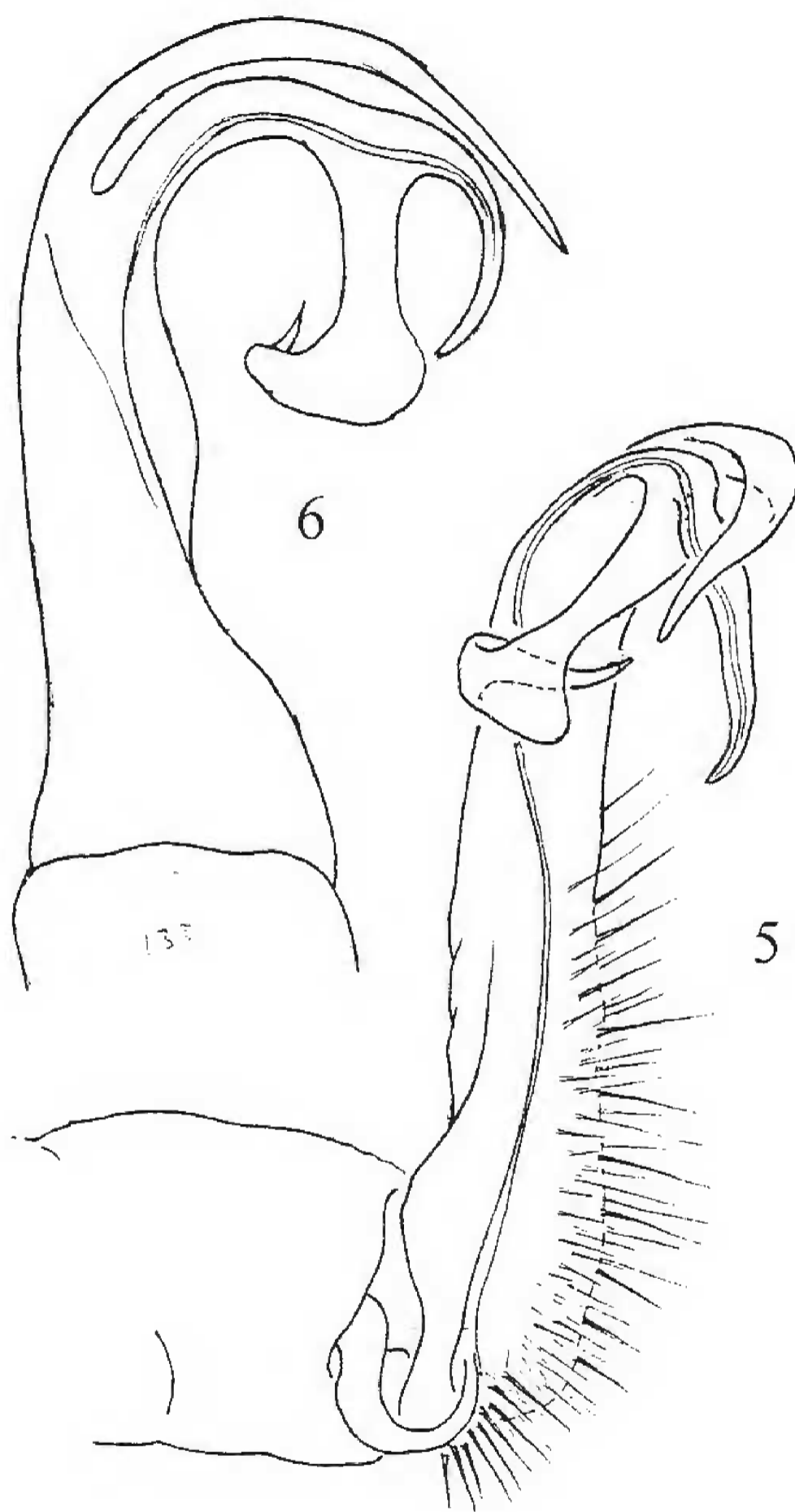
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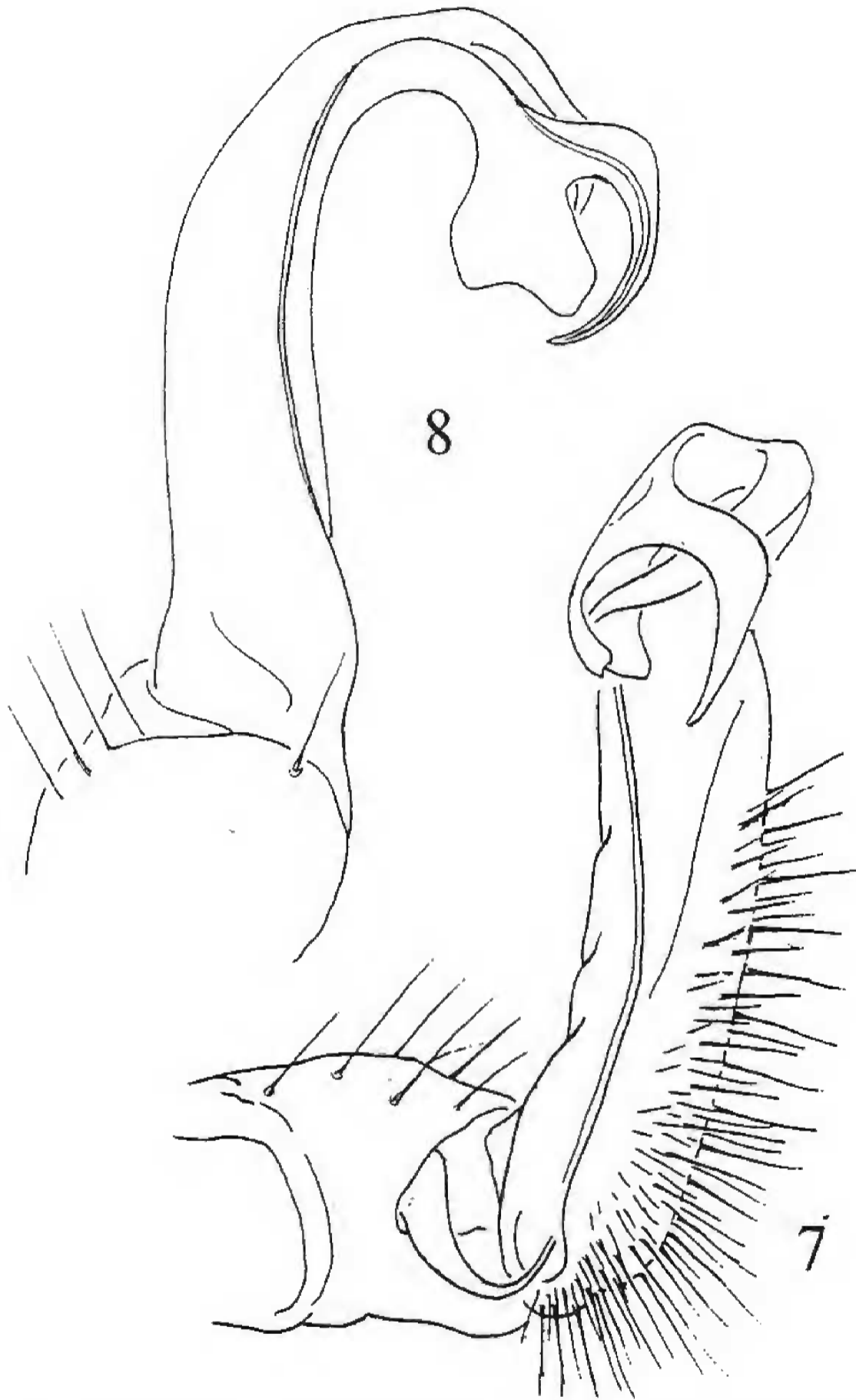


Figs. 2-4. *Zodesmus tuberosus* (Pocock), topotype male from "Kei" islands. 2. Left gonopod, mesal aspect. 3. Left gonopod, dorsolateral aspect. 4. Left side of segment 10, dorsal aspect.

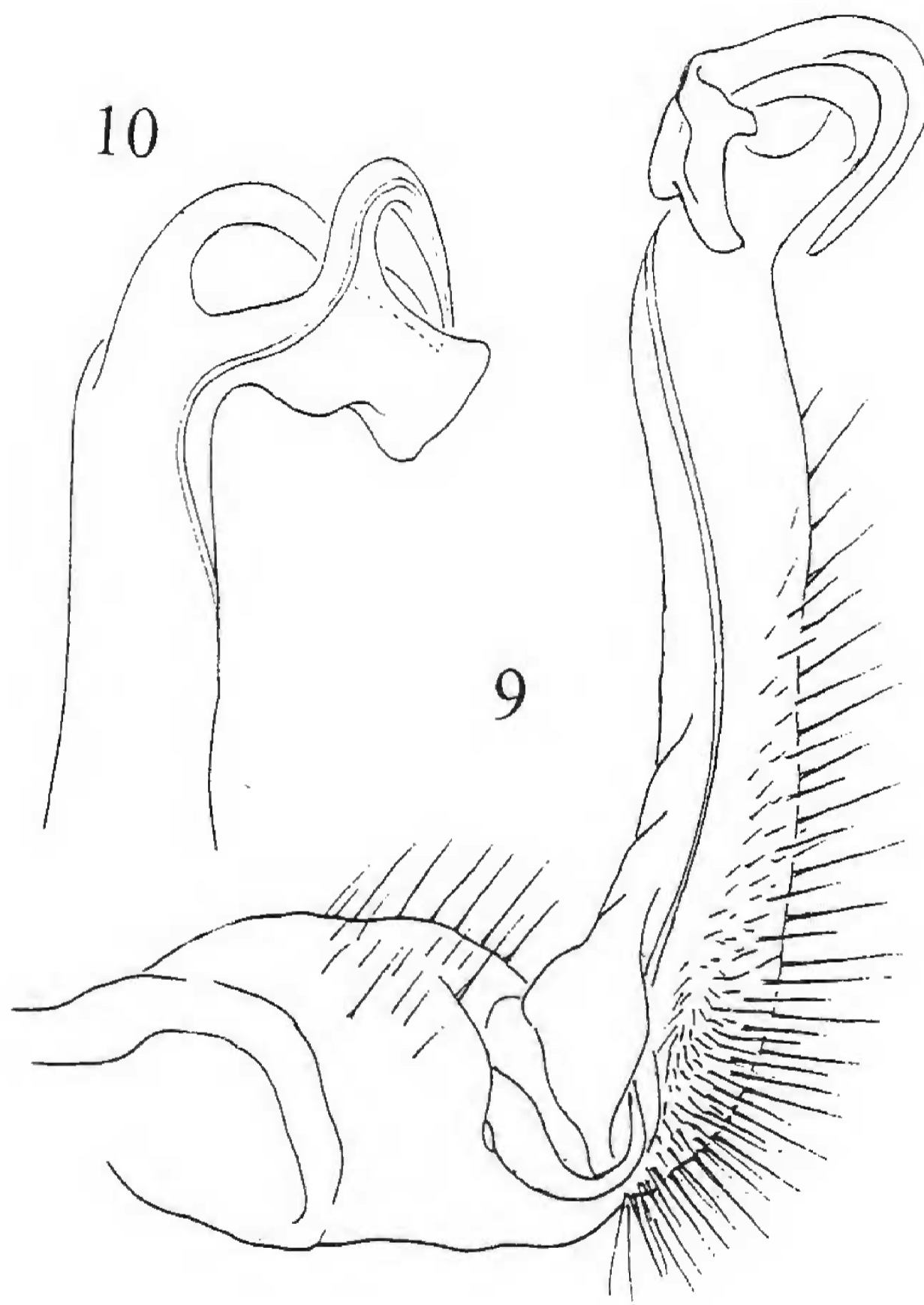




Figs. 5, 6. *Zodesmus stenotrichus* (Attems), syntype from Sakoemi, Irian Jaya. 5. Left gonopod, mesal aspect. 6. Left gonopod, dorsolateral aspect.

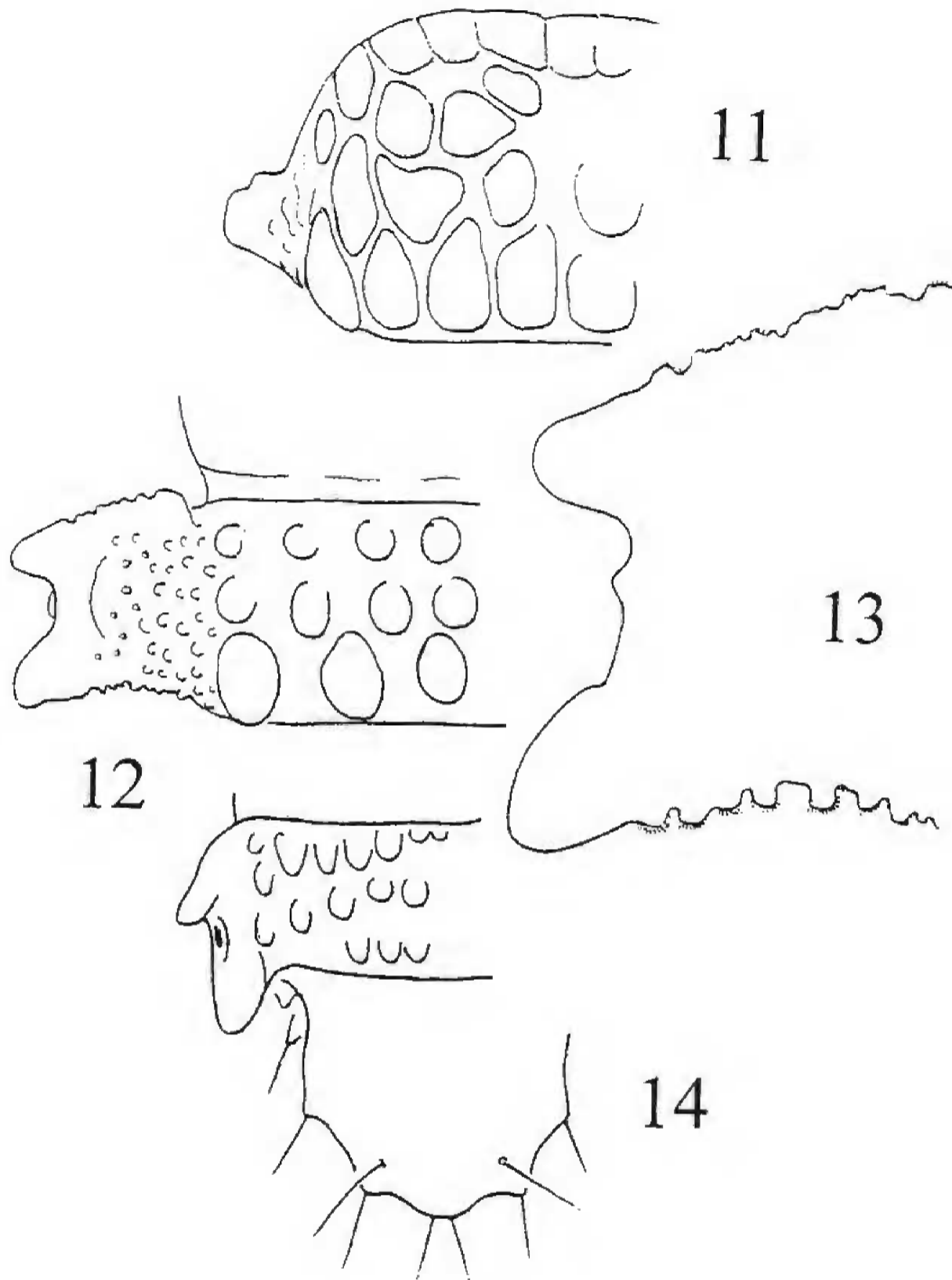


Figs. 7, 8. *Zodesmus margaritatus* (Pocock), lectotype. 7. Left gonopod, mesal aspect. 8. Left gonopod, dorsolateral aspect.

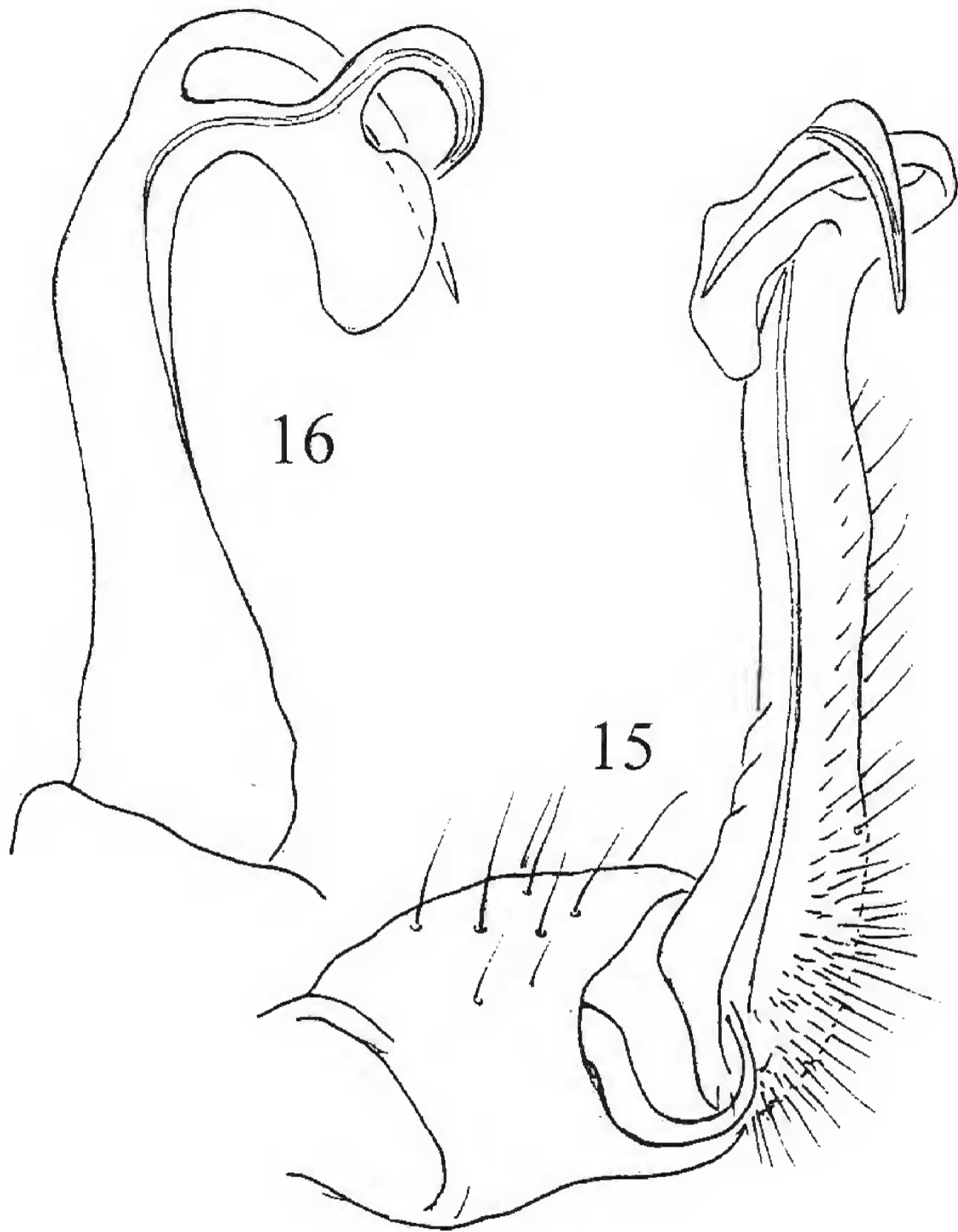


Figs. 9, 10. *Zodesmus lobophorus* (Attems), syntype male from upper Sepik River, Papua New Guinea. 9. Left gonopod, mesal aspect. 10. Left gonopod, dorsolateral aspect.





Figs. 11-14. *Zodesmus astromontis*, n. sp., holotype. 11. Left side of collum, dorsal aspect. 12. Left side of segment 10, dorsal aspect. 13. Left paranotum of segment 10, enlarged to show crenulation of edges. 14. Epiproct and paranotum of 19th segment, dorsal aspect.



Figs. 15, 16. *Zodesmus astromontis*, n. sp., holotype. 15. Left gonopod, mesal aspect.  
16. Left gonopod, dorsolateral aspect.